

QUEEN REPLACEMENT IN DEQUEENED COLONIES
OF THE ARGENTINE ANT
IRIDOMYRMEX HUMILIS (MAYR)

BY LUC PASSERA,¹ LAURENT KELLER² AND JEAN-PIERRE SUZZONI¹

INTRODUCTION

Replacement of killed or damaged queen by a new inseminated queen produced in the same nest is regularly accomplished in honey bees (Butler, 1967; Wilson, 1971; Michener, 1974). In the lower termites, e.g., *Calotermes*, it has been known for a long time that the removal of the sexual pair leads to the differentiation of neotenic reproductives from larval, pseudergate or nymphal forms (Grassé and Noirot, 1946; Nagin, 1972). In the higher termites, e.g., *Nasutitermes*, dequeened societies may produce either neotenic reproductives or differentiate young alates who have fully developed wings (Harms, 1927; Noirot, 1956, 1969; Thorne, 1982; Roisin and Pasteels, 1986).

In contrast, the replacement of queens by new inseminated queens produced in the same nest is very rare in ants. When colonies are orphaned, workers often start to lay eggs (see review in Passera, 1984) but these eggs are not fertilized and therefore develop into males. Furthermore, after a colony has been dequeened, it often starts to rear queen larvae, then produces virgin queens (Passera, 1984). But these virgin queens are not inseminated and thus may not replace the absent mated queens. Insemination generally occurs only during the nuptial flight. The probability that winged queens will return to their natal society after the nuptial flight is very low.

The aim of this study was to determine whether queen replacement occurs in dequeened colonies of *Iridomyrmex humilis*.

MATERIAL AND METHODS

Large societies of the Argentine ant were collected in December 1985 in Port-Leucate, near Perpignan, in Southern France. These

¹Laboratoire d'Entomologie, Université Paul-Sabatier, 118 route de Narbonne, 31062 Toulouse Cedex, France.

²Musée zoologique, Palais de Rumine, CP 448, Lausanne 17, Switzerland.

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societies considered as stock colonies were kept in large plastic boxes and reared in conditions similar to those described in Passera *et al.* (1988).

Forty-seven experimental queenless units were constituted by splitting four queenright stock colonies from 10/12/85 to 23/5/86. Each experimental unit consisted of about 650 workers and brood ranging from eggs to worker pupae. The brood was carefully monitored with the aim of avoiding the introduction of differentiated sexual larvae which are easily distinguished from worker larvae on the basis of size and/or color. Queen larvae never develop in queenright colonies (personal observation) so they were not present in any of the stock colonies. Moreover their matt color and their large size contrast sharply with those of the worker larvae. Male larvae are periodically produced in such stock colonies (Passera *et al.*, 1987) in the presence of the queens, so we selected periods when they were absent. The experimental units were then monitored daily for the presence of sexual forms.

RESULTS

Males: Of the 47 experimental units, 44 (93.6%) produced male larvae. This is explained by the fact that male brood is always present in stock colonies but its development is dependent on the trophic status of the society. This trophic status depends on the worker/larva ratio and/or queen number per colony (Passera *et al.*, 1988). Males pupated between the 7th and 95th day after the beginning of the experiment ($N = 758$; mean in days \pm SD = 38 ± 15). So the period of emergence of males is rather broad.

Queens: Thirty-seven of the 47 experimental units (78.7%) produced queen larvae. In queenright societies queen larvae were never produced whatever the brood composition or trophic status.

Queen production was not dependent on the season. In December the brood used in experimental units was a little overwintered but the brood used later in spring was supplied by stock colonies kept at a high temperature (28°C) in the laboratory for several months. In both cases the experimental units produced queen larvae. This differs from other ant species in which sexuals forms generally develop only from overwintered brood (Passera, 1984).

Queen larvae differentiated 24 to 53 days after the queens were removed. The first queen larvae were produced only after 24 days

because caste determination occurs very early at the beginning of the larval stage (Passera and Keller, unpublished data). Consequently, pupation of female sexuals occurred no earlier than day 32 and continued as far as day 84 ($N = 94$; mean \pm SD = 56 ± 8). Winged virgin queens emerged later ($N = 28$; mean \pm SD = 64 ± 12).

Mating and colony growth: At the time of the emergence of virgin queens there were always males of varied age because of the broad period of their emergence. On the other hand, the number of males was always large because the sex ratio favors these later: a total of 758 male pupae and only 94 queen pupae were produced over all the experimental units.

Of the 38 winged queens monitored, 36 (95%) succeeded in copulating with males in the nest. This is explained because in this species there is no mating flight (Newell and Barber, 1913; Markin, 1970; Benoist, 1973) and mating usually occurs in the nest.

In our experimental units, copulation occurred very quickly after queen emergence: 5.1 ± 1.9 days ($N = 36$) after emergence queens were dealated and egg laying by queens began immediately. The number of remaining workers was greatly decreased, but was still large enough to rear the new brood. The first callow workers emerged about 50 days after queen mating and about 130 days after the societies were dequeened.

DISCUSSION

The production of virgin queens in queenless societies has been demonstrated in a number of species including *Hypoclinea quadripunctatus* (Torossian, 1967), *Plagiolepis pygmaea* (Passera, 1969, 1984), *Leptothorax nylanderi* (Plateaux, 1971), *Leptothorax recedens* (Dejean, 1974), *Odontomachus haematodes* (Colombel, 1978), *Camponotus aethiops* (Dartigues, 1978; Suzzoni *et al.*, 1986), *Myrmica rubra* (Brian, 1979, 1983), *Solenopsis invicta* (Vargo and Fletcher, 1986). In all these cases, the new virgin queens were never inseminated inside the nest resulting in the failure of the replacement of the mated queen. The replacement of mated queens has been reported in only three species.

The first case is the red imported fire ant *Solenopsis invicta* (Tschinkel and Howard, 1978). When monogynous colonies in the field are orphaned by removing the queens, censuses made several

weeks later, often show the presence of a new inseminated egg-laying queen. But the process of the regulation is different than in *I. humilis*: the replacement queens does not originate from a new rearing of sexual larvae. Rather they were probably surviving foundresses remaining in the societies after the pleometrotic colony founding, which leads the authors to hypothesize that these societies were functionally monogynous.

The second case of regulation exists in *Cataglyphis cursor*. The mechanism is again completely different than in *I. humilis*. In the laboratory, workers in queenless societies lay arrhenotokous eggs which develop into males and thelitokous eggs which develop into queens (Cagniant, 1976). After mating, which occurs near the nest at ground level (Cagniant, 1976), queens return to their society. By this mechanism, societies display the ability to replace the mated queen when she is experimentally removed in field colonies (Lenoir *et al.*, 1986).

The third case of queen replacement is found in *Monomorium pharaonis* which displays a similar mechanism as in the Argentine ant; namely when societies are dequeened, males and winged queens are produced and mate within the nest (Peacock and Baxter, 1949; Petersen-Braun, 1975).

Hence, *M. pharaonis* is the only species which displays a similar mode of queen replacement as the one described in *I. humilis*. Such a mechanism involves three factors:

—Mating must occur within the nest or in the immediate vicinity. This condition involves a polygynous colony structure as occurs in both *M. pharaonis* and *I. humilis*. Several pairs of closely related species are known, one being monogynous and the other polygynous, e.g., *Myrmica ruginodis*, *macrogyna* and *microgyna* (Brian and Brian, 1955), *Pseudomyrmex ferruginea* and *P. venefica* (Janzen, 1973), *Lasius niger* and *L. sakagami* (Yamauchi *et al.*, 1981). In these three pairs, the first species is monogynous and queens mate outside the nest during a nuptial flight, whereas the second species is polygynous and queens often mate within the nest. In monogynous species, mating within the nest is probably selected against because the deleterious effect of inbreeding (Bruckner, 1980; Brian, 1983). On the contrary, in polygynous species in which sexuals are produced by several queens, e.g., *I. humilis* (Keller, unpublished data), mating within the nest is possible without a high degree of inbreeding.

—In queenless colonies, female brood may develop into queens at any time of the year.

—Male brood always exists in societies and generally develops into males when the societies are dequeened.

These three conditions being infrequently connected within a species renders queen replacement a rather rare phenomenon in ants.

SUMMARY

When experimental societies of the polygynous ant *Iridomyrmex humilis* were dequeened, they produced both male and queen larvae. This production of sexuals may occur at any time, because the differentiation of sexuals is not connected with overwintering of the brood.

The emergence of queens occurred about 70 days after queen removal, whereas males emerged generally earlier. Since mating flights are lacking in this species, the newly-produced virgin queens and males copulated within the nest less than 8 days after emergence of queens. Then newly inseminated queens began to lay eggs rapidly after mating and the first callow workers emerged 50 days later.

This form of social regulation is rather uncommon in ants. Factors allowing this regulation are discussed.

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